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pH-dependent absorption of solutions by the ventral tube of *Tomocerus flavescens* (Tullberg, 1871) (Insecta, Collembola) *

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Synopsis : *Tomocerus flavescens*, a beech litter dwelling species, uses its ventral tube vesicles to aborb liquid water and buffer solutions. Different experiments show that all individuals display an acidophobic reaction at low pH (pH 3, pH 2), and liquid absorption increases when pH values reach 5 and 6, then decreases towards the alkaline range. The authors comment the absorptional behaviour of Tomorecus flavescens in relation to the fecundity, development and longevity in other species, then enlarge the discussion upon the consequences of soil acidification on the water balance in Collembola.

Keywords : pH, absorption, water balance, ventral tube, *Tomocerus flavescens*, Collembola.

INTRODUCTION

According to their vertical distribution and their specific adaptations to terrestrial life most Collembolans belong to the community of the euedaphon and the epedaphon. The majority of species has adapted to high degrees of ambient and substrate humidity and can be typified as extremely hygric or hygric humid-air animals (EISENBEIS, 1983; EISENBEIS and WICHARD, 1985), which are often dependent on permanent contact with water. The same is valid not only for the euedaphic species but also for the inhabitants of extreme biotopes, for example glacier Collembolans or epineustic forms. With reference to the requirements of humid-air animals, Collembola show

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special adaptations concerning the regulation of their water balance. Considerable water losses may due to transpiration even at a small deficit in their ambient humidity and even in a water vapor saturated environment. For instance, the euedaphic *Onychiurus* from a beech forest soil loses from its water mass (at 22° C) with average rates of 7 %/h at 100 % r. h., 17 %/h at 98 % r. h. and 95 %/h at 76 % r. h. In epedaphic Collembola, for example in *Tomocerus* and *Orchesella*, the average loss amounts to 9 %/h and 6 %/h respectively at 76 % r. h./22° C.

The ventral tube operates as the central organ of extraoral water uptake with the help of the animals absorb water from moist surfaces, e. g. leaves, bark or even artificial substrates (EISENBEIS, 1982). The tube vesicles are easily moistened whereas the body cuticle cannot be moistened due to its ~~ela~~borate surface structures and its wax coating. Beneath the thin cuticle of vesicles there is a transport epithelium a few µm thick immediately bordering on the hemolymph cavity (EISENBEIS, 1974; WEISSGERBER, 1983). Previous experiments showed an influence of salinity and temperature on the uptake rate of water (BLEICHER, 1981; EISENBEIS, 1982; WEISSGERBER, 1983). The present study aims at showing whether the pH of solutions has any significance for the absorption and whether conclusions can be drawn from acidification of soils on the water balance in Collembola.

I. — MATERIAL AND METHODS

Tomocerus flavescens (TULLBERG, 1871) were collected from beech forest litter in the West German Taunus area. The animals were kept in boxes together with moist leaves. To maintain a high ambient humidity the bottoms of the boxes were covered with a mixture of plaster and charcoal. The weight of the animals ranged from 2.5 to 6 mg.

A) Measuring transpiration.

Weight loss was measured with a recording electrobalance (SARTORIUS type 4436, sensitivity 1 µg, with automatic taring) which was modified for « underfloor » measurement (EISENBEIS, 1982). The test specimen was put to a small cage which was placed into a 25 ml-sized glass vial and connected to the balance. In this vial, a relative humidity of 33 % was maintained at 20 °C by means of a saturated solution of $MgCl_2$ (WINSTON and BATES, 1960). Immediately after exposure the initial weight (w_0) of the animal was taken, then the balance was tared and the loss of weight by transpiration could be recorded continuously (Fig. 1). At the end of the first transpiration phase, a defined deficit of water occurred which stimulates Collembolans to absorb water by means of their ventral tube. A deficit of 20 % of the initial water mass of the animal (m_0) proved favourable. This quantity could easily be determined after measuring the initial weight (w_0), because the water content of normally hydrated animals amounts to nearly 80 % of the total weight. After reaching the precalculated loss of weight, the balance was locked and the animal was removed for the subsequent absorption experiment. The last weight value was stored in the balance during this period. After absorption the animal was put back into the balance and the weight gain was recorded immediately (Fig. 1).

B) Measuring absorption.

In order to find out the absorption rate, the test animal was removed from the balance and put on filter paper (Ø 25 mm) which had been placed on the bottom of a closed

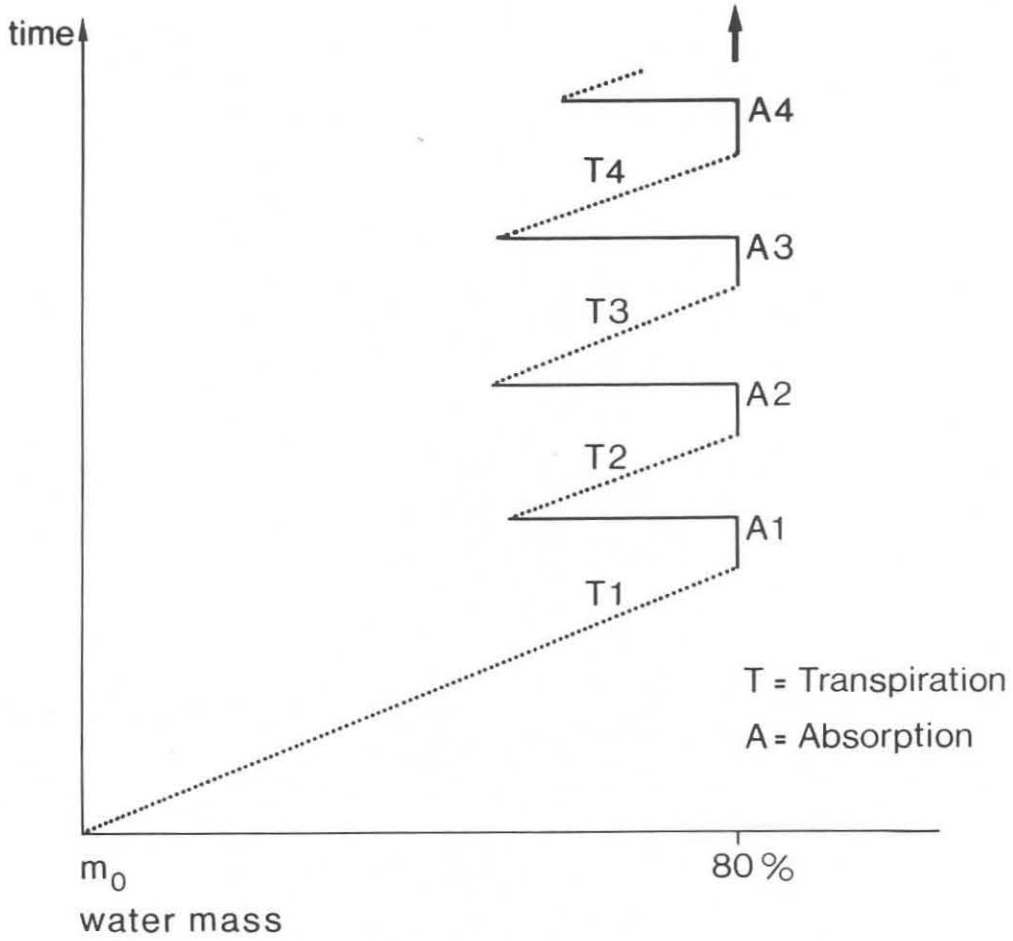


FIG. 1. — Measurement of weight changes by transpiration and absorption in *Tomocerus flavescens*. The experimental pattern is derived from recorded graphs. In a first step the initial water mass m_0 (= 100 %) of the animal is reduced to a level o 80 % (transpiration phase T 1). Then the first absorption phase (A 1) follows, recorded as gain of weight. Successive transpiration and absorption phases alternate during the experiment, in which the solutions used for absorption can be changed.

glass-vial (volume 25 ml). The filter paper was moistened with 100 µl of buffer solution (phosphate or citric acid buffer) at the beginning of the experiment. The solutions of the phosphate buffer (prepared by 0.2 M NaH_2PO_4 and 0.2 M Na_2HPO_4) had pH values of nearly 4.5, 5, 6, 7, 8, 9 and the citric acid buffers (prepared by 0.1 M citric acid and 0.2 M Na_2HPO_4) were adjusted to nearly pH 2, 3, 4, 5, 6, 7, 8 and 9 (GEYER, 1973; HALE, 1966). The osmolality of all solutions was adjusted to 50 mOsm by dilution with aqua dest. The animals were observed during the absorption phase (10 min). It became apparent that the vesicles of the ventral tube were pressed onto the moist filter paper. Usually the animals absorb continuously. In some cases, the absorption process was interrupted briefly by retraction of the vesicles. In these cases, a ten-minute absorption was achieved by recording only the actual absorption time. The interruptions became more frequent on increasing the acidity of the substrate. Especially at pH 2, the animals showed acidophobic behavior. The temperature for the absorption was adjusted to 20° C.

After finishing the absorption, the animal was put back into the cage of the balance immediately and the increase in weight was measured (Fig. 1). Subsequently, another transpiration phase followed up to the level of 80 % of the water content when a second absorption phase could be started. Usually, an animal had to absorb four times. There

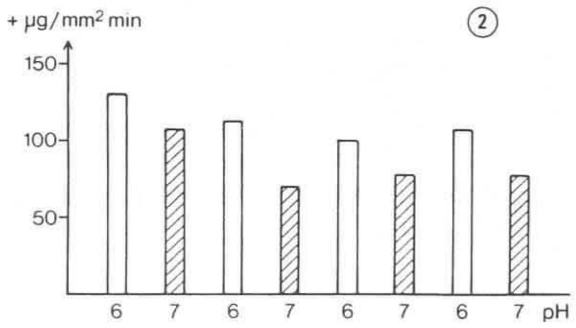
were even up to ten successive absorption phases with some animals in order to discover changes of absorption rates during the experiment. In the few cases of oral uptake of fluid the measurements were ignored.

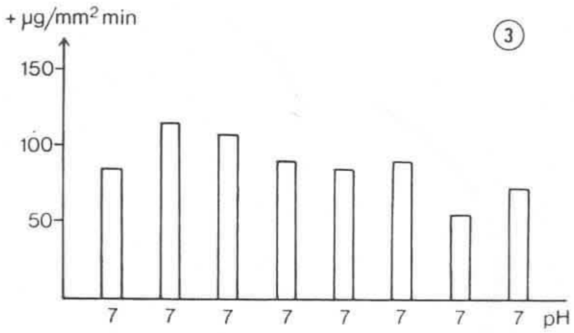
The weight gain by absorption was either calculated in absolute rates ($\mu g/mm^2 \cdot min$) or in relative rates (Δ m %/h) with reference to the water mass m_0 of normally hydrated animals. The effective surface of ventral tube vesicles ($S_{Vt\text{-}eff}$) used for the absorption can be calculated by the equation: $S_{Vt\text{-}eff} = w_0 \cdot 0.0547$ (mm^2) (EISENBEIS, 1982). The weight losses which occurred during the removal from the balance and the return to it were insignificant. During absorption the animal was placed in a water vapor saturated atmosphere in order to avoid weight loss by transpiration.

II. — RESULTS

A) Behavior of individuals during absorption.

If the animals are put onto the moistened filter paper after their transpiration phase, they ever their ventral tube after a few seconds and remain motionless. They absorb for 15-30 minutes, or even longer in some cases, without interruptions, if they are not disturbed. In our experiments, absorption was stopped after 10 minutes. The animals accept the offered 50 mOsm buffer solutions of phosphate and citric acid buffer and behave in the same way as during absorption of pure water. At pH 2 however, they evert their





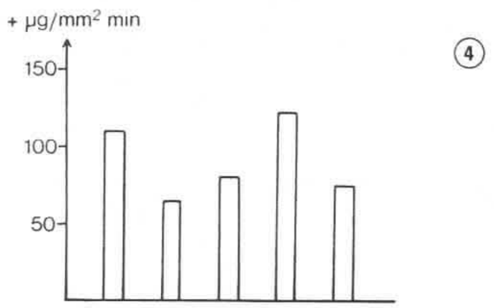


FIG. 2. — Successive absorptions by the ventral tube of a specimen of *Tomocerus flavescens* from phosphate buffer (50 mOsm) at pH 6 and pH 7.

FIG. 3. — Successive absorptions by the ventral tube of a specimen of *Tomocerus flavescens* from phosphate buffer (50 mOsm) at pH 7.

FIG. 4. — Successive absorptions by the ventral tube of a specimen of *Tomocerus flavescens* from filter paper moistened with different amounts of solution (citric acid buffer at pH 8).

ventral tube vesicles repeatedly for short periods followed by retraction. This can be repeat several times during which the animals move restlessly to and fro.

The maximum rate of absorption is reached during the first three absorption phases. The same result was pointed out by EISENBEIS (1982) on measuring the uptake rates in *Tomocerus* at different salinity levels and for pure water. If a higher number of absorptions is performed in close succession, the uptake rate steadily decreases as a rule. Fig. 2 and 3 demonstrate this phenomenon with two specimens placed on phosphate buffers at a change between two pH steps (pH 6 and 7) and at the same pH (pH 7).

B) Absorption dependent on the quantity of fluid.

Preliminary experiments were carried out in order to determine whether the quantity of fluid in the filter may affect the rate of absorption. The filter paper was entirely saturated with 100 μl of solution and there was enough free solution between its fibres. An additional quantity of fluid provided to a continous fluid surface. When only 30 μl was applied, the solution was completely absorbed from fibres and the contact of the tube vesicles with free solution could not be achieved. Hence, the experiments were carried out with 100 μl buffer solution in the filter paper. The change ~~of~~ uptake rates influenced by different quantities of solution in the filter is shown in Fig. 4.

C) Absorption of phosphate buffer at 20° C.

The absorption of phosphate buffer was tested over a range of pH 4.5 to 9. A lower pH could not achieved by means of this buffer. The maximum absorption is achieved at pH 6 with $107 \pm 44.2\ \mu g/mm^2 \cdot min$ ($\pm$ S. D.). Fig. 5 shows the change of the average rates. In no case do the adjacent rates differ significantly. However, on comparing the rates of pH 4.5 and pH 6, there is significance for $P < 0.05$. Additionally, the average rates of the first four absorption periods of specimens are given (Fig. 5, dotted columns). Except in pH 4.5, there are slightly higher mean values in this calculation. Beginning with pH 6 the rates decrease towards the acidic as well as towards the basic range. In pH 8 the decrease amounts about 30 % of the maximum rate, whereas in pH 9 there is a rise in the average rate. But the data vary considerably in this case.

D) Absorption of citric acid buffer at 20° C.

The citric acid buffer was accepted also by *Tomocerus*. The buffer solutions were adjusted from pH 2 to pH 9. The average rates of all experiments are combined in Fig. 6. There is evidence of a nearly linear rise of rates from pH 2 to pH 6. Furthermore, there is, similar to the phosphate buffer, a decrease to the low basic range of pHs, but no increase at pH 9. The average rates of pH 2 compared to pH 5 differ considerably ($P = 0.001$), in adjacent pH steps the t-test proves significance only between pH 3 and pH 4.

During the absorption of pH 2 and pH 3 buffer, the animals often showed acidophobic behavior. There were several interruptions during absorption. The tube with its vesicles touched onto the filter paper for only a few seconds followed by retraction. Only a few animals reached an absorption time of ten minutes.

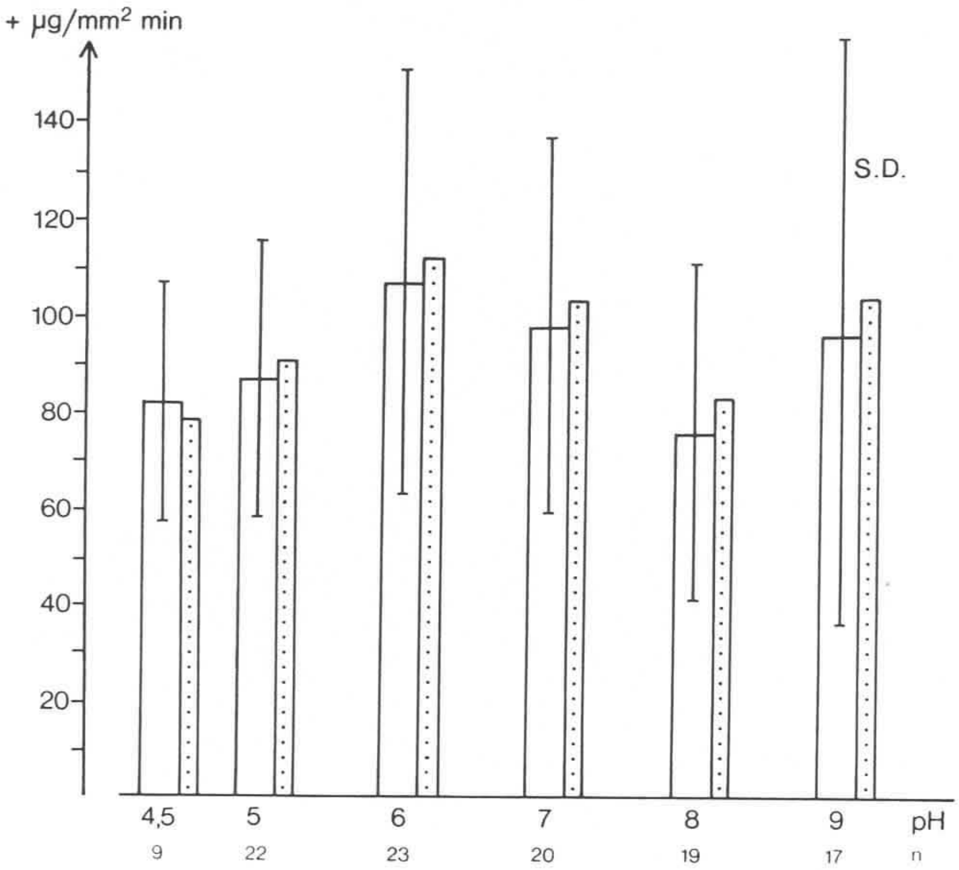


FIG. 5. — Average absorption rates by the ventral tube of *Tomocerus flavescens* from phosphate buffer (50 mOsm) at different pH. The open columns include the data of all experiments, the dotted columns show the average rates of the first four absorptions of animals.

E) **Effect of absorption on the change of water mass.**

During the transpiration phases the initial water mass of *Tomocerus flavescens* decreased by an average of 15 %/h at 33 % r.h./20°C. On the other hand, the absorption by the ventral tube causes a fast increase of the water mass. In the case of pure water, the uptake rate amounts to about 60 %/h (EISENBEIS, 1982). If the 50 mOsm buffer solutions are used, the osmotic effect reduces the uptake (Fig. 7) which is also influenced by the pH. In pH 5 the average uptake rate amounts to 40 %/h whereas it is only 20 %/h in pH 2. This means, that in pH 2 the refill of water takes place in half the time. Nevertheless, the resulting uptake rate at pH 2 is slightly above the transpiration rate which occurs at lowered humidity.

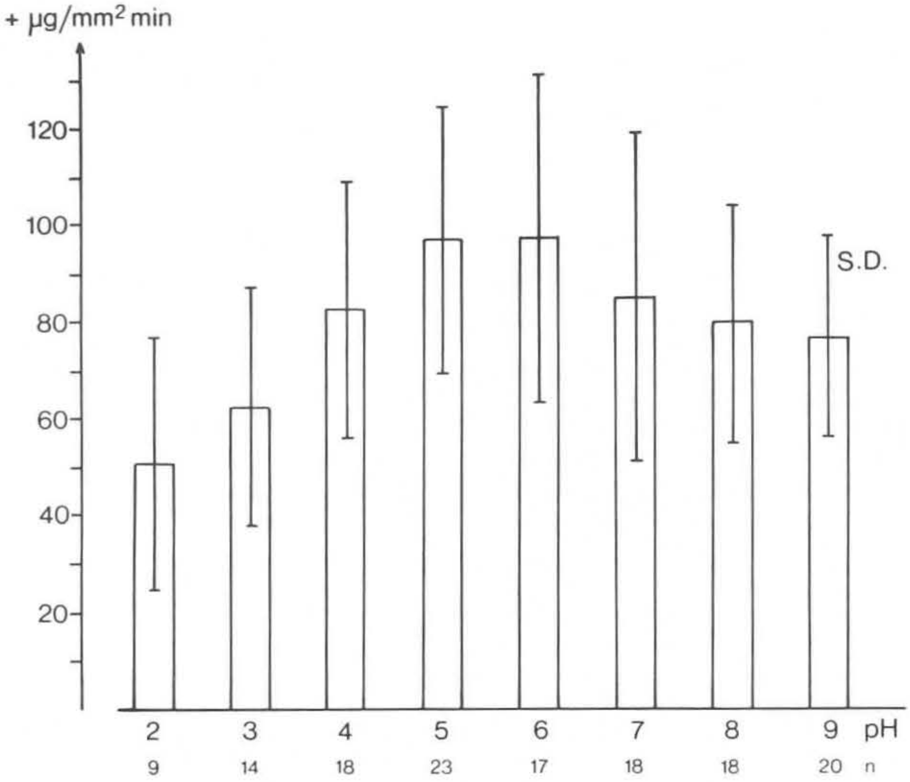


FIG. 6. — Average absorption rates by the ventral tube of *Tomocerus flavescens* from citric acid buffer (50 mOsm) at different pH.

F) **pH determinations of organic samples from Beech forest.**

Litter samples were taken monthly (May 1982 to March 1983) from the habitat of *Tomocerus flavescens* (Beech forests in the Taunus region near Schlangenbad) and the pHs determined by three methods. The following data give the range of measured pHs:

Beech litter		Beech litter*		Beech raw humus*	
pH_{CaCl_2}	3.6 — 4.6	pH_{CaCl_2}	3.4	pH_{CaCl_2}	3.6
pH_{KCl}	3.9 — 4.8	pH_{KCl}	3.3	pH_{KCl}	3.4
pH_{H_2O}	4.3 — 5.6	pH_{H_2O}	4.1	pH_{H_2O}	4.6

III. — DISCUSSION

A) Absorption behavior of *Tomocerus flavescens*.

Similarly to earlier experiments, when the uptake rate of pure water or saline solutions was tested (EISENBEIS, 1982), *Tomocerus* absorbed the buffer solutions offered during the initial absorption phases at slightly

* Data from the Taunus region published by KRIETER (1982).

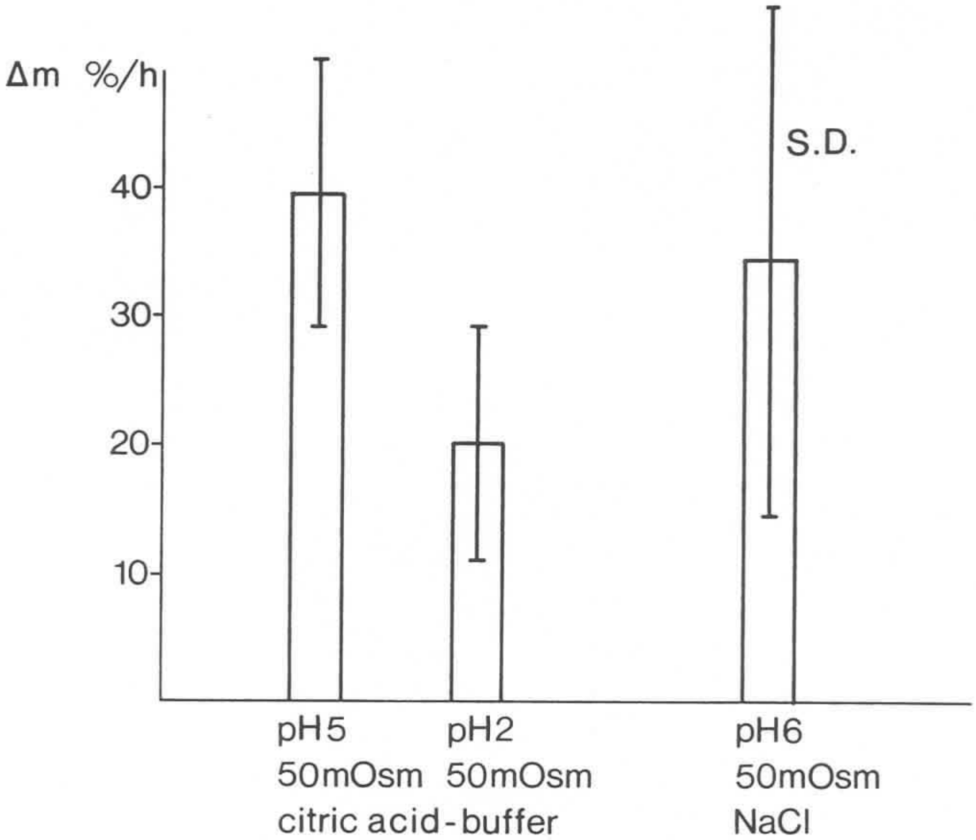


FIG. 7. — Changing of the animals water mass by absorption of the ventral tube from different substrate solutions in *Tomocerus flavescens*. The average uptake rates are expressed as changes in the water mass per hour (Δ m %/h) related to the initial water mass m_0. The uptake rate from the NaCl-solution is derived from EISENBEIS (1982).

increased rates which afterwards decreased gradually in most cases. Before each of the absorption phases, the animals were at the same level of hydration (see Fig. 1). Hence, we would expect a comparable composition and concentration of hemolymph. The decrease of the absorption efficiency may be caused by changes of the transport epithelium. Its high content of mitochondria in close connection with membrane invaginations (EISENBEIS, 1974) suggests the existence of a secondary mechanism of water resorption, perhaps coupled to an ion transport, in addition to the primary passive osmotic component of water uptake. A repeated stress or shock effect on the epithelium by high water influx may affect this energy dependent component. The large variation of absorption rates in general may be explained by the fact that the used animals were not synchronized in respect to the moulting cycle. Earlier experiments showed that absorption is considerably reduced before the moult (EISENBEIS, 1982). At that time the tube vesicles are covered with a double cuticle and the apical cell border of transport cells, i. e. the microfolds, are reduced in size. The absorption characteristics vary even during the intermoult phase. Animals after ecdysis (cultured under defined laboratory conditions), which possess a new cuticle on the vesicles, show a nearly total permeability barrier towards certain organic molecules, e. g. urea, whereas the permeation increases again during the intermoult phase (SCHREIBER,

1983). In animals taken immediately or some days earlier from their habitats, the ventral tube often proved to be leaky with respect to the urea intake. SCHREIBER interpreted this phenomenon as an « abrasion effect » of the cuticle. Accordingly, great importance is attributed to the cuticle as a permeation barrier. Perhaps its contact with rough substrate surfaces in the field leads to more mechanical strain on the epicuticle producing permeable pores.

In a highly acidified artificial substrate, e. g. the citric acid buffer, the animals show an increase in acidophobic behavior. In pH 3, this response is still relatively rare whereas it dominates in pH 2. Probably the animals perform a test of the substrate by briefly everting their ventral tube and retract their vesicles from the acid substrate at once. This can occur repeatedly while the animals run restlessly to and fro. Afterwards the ventral tube remains retracted in many cases. The ciliary sense organs which are integrated into the epithelium of the vesicles are considered to be sensors for substrate testing. EISENBEIS (1976) suggested that they are osmo- or hygroreceptors. Acidoreception seems to be likely in the light of the discussed observations.

At higher pH, animals in most cases immediately absorb continously after the first « touch down » of their vesicles. Sometimes repeated substrate testing were performed by eversion and retraction of vesicles. Even in pH 9 animals showed normal behavior. The phosphate as well as citric acid buffers proved to be favourable to the performance of experiments because the animals absorbed them in the same way as pure water. The chosen pH range between pH 2 and pH 9 includes both the physiological range and pHs from habitats in the field. The latter were found primarily in the acid range because the pH of acid precipitations amounts between pH 2 and 3 in areas of industrial pollution and even the active acidity of the soil surface can reach values which must be characterized as very acid (pH 4.9-4.0) or extremely acid (pH 3.9-3.0) according to the classification of soils of SCHEFFER and SCHACHTSCHABEL (1978).

B) **Reaction of Collembola to pH.**

The direct effects of acid to weak basic solutions on the absorption rates of the ventral tube were measured in our experiments. The maximum absorption of phosphate as well as citric acid buffers occur in the weak acid to moderate acid range (pH 5 to pH 6). The rates decrease towards the stronger acid and weak basic pHs. Whereas the rates further decrease in pH 8 to 9 with citric acid buffer, they rise once more with phosphate buffer. Possibly the thin transport epithelium is affected by the alkaline medium reducing the resistance to permeation which causes the higher osmotic water influx. However, the average absorption rates in the basic range do not differ significantly. Therefore, a definite interpretation is not possible. Relating the course of absorption rates of phosphate buffer to the preference curve of *Orchesella villosa* (MERTENS, 1975) there is evidence of a similar wavy curve. *O. villosa* preferably accumulates at pH 6, if the animals are placed along a pH gradient. Towards the acid and neutral range the numbers of animals decreases and then rises in the basic range once again. MERTENS interprets the latter as direct lesion by the basic milieu. The motoric acti-

vity of animals diminishes as they cannot easily change their position. On the other hand, the animals are very active in the acid range. They run restlessly to and fro actively seeking moderate acid milieu.

HUTSON (1978) investigated fecundity and longevity in relation to pH in four species of Collembola. Animals reacted differently according to species but longevity is longest at pH 4 to 6. The highest egg production takes place at pH 5 to 7. In three species, *Folsomia candida, Tullbergia krausbaueri* and *Isotoma notabilis*, the optimum of fecundity is located at pH 5.2. Only *Proisotoma minuta* reached its highest quantity of eggs at pH 7.2. Laboratory cultures of *Folsomia candida* which are parthenogenetic, and the acidophilic *Tullbergia krausbaueri* produce eggs even at pH 3.3, but only 10 % of the normal rate. Animals from the field population of *F. candida* reached their lower limit at pH 4.3. At pH 2.5 none of the four species examined produced eggs any more.

Sminthurus viridis, the lucerne flea, also has its optimum of growth and fecundity in the weak acid range (pH 6.0 to 6.5) (MACLAGAN, 1932). The time fore development is doubled at pH 4.1. In the pH gradient animals accumulate at pH 6.1 to 6.3. A change to acid pHs results in larger differences of fertility than in the weak alkaline milieu. A summary of results concerning direct effects of pH on Collembolans makes clear that the pH has great importance for the autecology and biology of these animals. Consequences for water balance must be expected in very acid to extremely acid substrates (pH < 3.9) because extraoral water uptake ability can be reduced to the half. This could be especially important during longer periods of drought when only substrate adsorbed or thin films of water are available from soils, leaves and bark. An interesting result is that optimum pH values with regard to fecundity, development and longevity of Collembolans as well as to the efficiency of the ventral tube are nearly identical and are located in the weak acid sphere (pH 5 to 6).

C) **Reaction of soil fauna to pH.**

According to former concepts (AGRELL, 1941; KÜHNELT, 1950; SCHALLER, 1962), pH has a subordinate effect on the occurrence of soil animals. Humidity, light and temperature are considered as prime factors of limitation with reference to life activities of these animals. CAMPELL (1981) holds the general view that pH of soil is of high ecological relevance to fauna as well as flora. Recent investigations of HAGVAR *et al.* (1980, 1981) on the effects of artificial rain and liming on some soil fauna reveal unequivocally that although species react differently, their biological activities are affected by pH shifts in all cases. These field and greenhouse experiments, mainly restricted to Acari and Collembola, led to a distinction between acidophilic, basophilic and indifferent species. In the course of colonization and field experiments with differently acidified substrates the highest number and abundance of species occured in birch litter acidified by artificial acid rain and raw humus of spruce (HAGVAR and ABRAHAMSEN, 1980; HAGVAR and AMUNDSEN, 1981; HAGVAR and KJØNDAL, 1981) in which case especially Oribatei met favourable conditions. Some species of Collembola, e. g. *Tullbergia krausbaueri* s. l., also reacted to acid substrate with increased abundance. On the

other hand *Isotoma notabilis*, *Frisea mirabilis* and *Onychiurus armatus* positively reacted to rising pH even after liming whereas *Lepidocyrtus cyaneus* proved to be indifferent to this treatment. Altogether the number of Collembolans diminished from pH 6 to pH 2 by 16 %, the total number of microarthropods showed a 53 % increase after acidification especially due to an increase in Acarids. HAGVAR *et al.* presume a correlation between pH of soils and the reproduction process. But it must be noted that soil type plays a role in population dynamics, too. Parallel to the field study, greenhouse experiments were performed with 10 mm of acid rain applied twice a week. In these treatments, classified as « shock effects », the abundance of most Collembolan species was drastically reduced. In many species of Oribatei a reduction was also noted, the total abundance of Oribatei, however, remained constant.

The acidification of soils caused by industrial and technical emission becomes more and more important especially with regard to its harmful effects on vegetation (BUTZKE, 1981; ULRICH, 1982). Investigations on changes in soil fauna demonstrate that species and higher taxa react to changes in pH very differently. Acarids seem, in general, to be less sensitive to acidification than Collembolans. The present study reveals that a specific physiological quality in *Tomocerus flavescens*, the ability to absorb water, can be affected by reduction of pH too.

SUMMARY

The ability of beech litter inhabiting Collembolan, *Tomocerus flavescens*, to absorb different buffer solutions with its ventral tube vesicles was tested. Two buffers were chosen to establish various pH values: phosphate buffer in a range of pH 4.5 to pH 9 and citric acid buffer in a range of pH 2 to pH 9. The animals absorb the buffers like pure water, an acidophobic response is visible only at strong acid pHs (pH 3, pH 2). The optimum uptake rates are in the upper acid range between pH 5 to pH 6. Then the rates decrease both towards the stronger acid and towards the alkaline range. At pH 2, the uptake rate is reduced to about a half. Soil acidification possibly influences the water balance of Collembola especially in dry habitat conditions. The optimum pH values for the absorption by the ventral tube in *Tomocerus flavescens* seem to correspond to those for the fecundity, development and longevity in other Collembolan species known from literature.

RÉSUMÉ

Les auteurs ont testé la capacité du Collembole *Tomocerus flavescens*, espèce de la litière de hêtre, à absorber différentes solutions tampons à l'aide des vésicules du tube ventral. Deux solutions tampons ont été choisies pour obtenir des valeurs variées du pH : une solution tampon de phosphate (de pH 4,5 à pH 9) et une solution tampon d'acide citrique (de pH 2 à pH 9). Les animaux acceptent les solutions tampons comme l'eau pure, mais une réaction acidophobe apparaît aux valeurs basses du pH (pH 3 et pH 2). Les taux d'absorption maximale ont lieu vers pH 5 et pH 6, puis les taux d'absorption décroissent aussi bien vers les pH acides que vers les pH alcalins. A pH 2, la vitesse d'absorption est réduite de moitié. L'acidité

des sols peut affecter la balance hydrique corporelle des Collemboles, plus particulièrement lorsque des conditions de sécheresse règnent dans les biotopes. Les valeurs optimales du pH pour l'absorption de liquide par le tube ventral chez *Tomocerus flavescens* semblent correspondre à celles, relatives à la fécondité, au développement et à la longévité, que l'on trouve dans la littérature pour d'autres Collemboles.

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